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The Relationships of the Rhachitomous Amphibian *Parioxys*

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The anatomy of the genus *Parioxys* from the Lower Permian of Texas has never been well known, and its taxonomic position has been subject to various interpretations. The species *P. ferricolus* was described by Cope (1878) on the basis of two poorly preserved skulls (A.M.N.H. Nos. 4309 and 2445). Cope later (1882) suggested that these specimens were young *Eryops*. Case (1911) and most subsequent writers have concluded, however, that the genera are distinct. Romer (1947), on the basis of partially prepared specimens of the type species in the Harvard collection, placed the genus in the family Trematopsidae. These specimens were later prepared and described by Moustafa (1955a). He placed the genus in a new family, Parioxyidae, and allied it with the Dissorophidae in the superfamily Dissorophioidea.

Recent work on the dissorophids (DeMar, MS; and Carroll, in press), as well as the discovery of an earlier and more primitive species of *Parioxys*, described below, necessitates a further look into the taxonomic position of the genus.

The names of institutions have been abbreviated as follows:

A.M.N.H., the American Museum of Natural History

M.C.Z., Museum of Comparative Zoölogy at Harvard College

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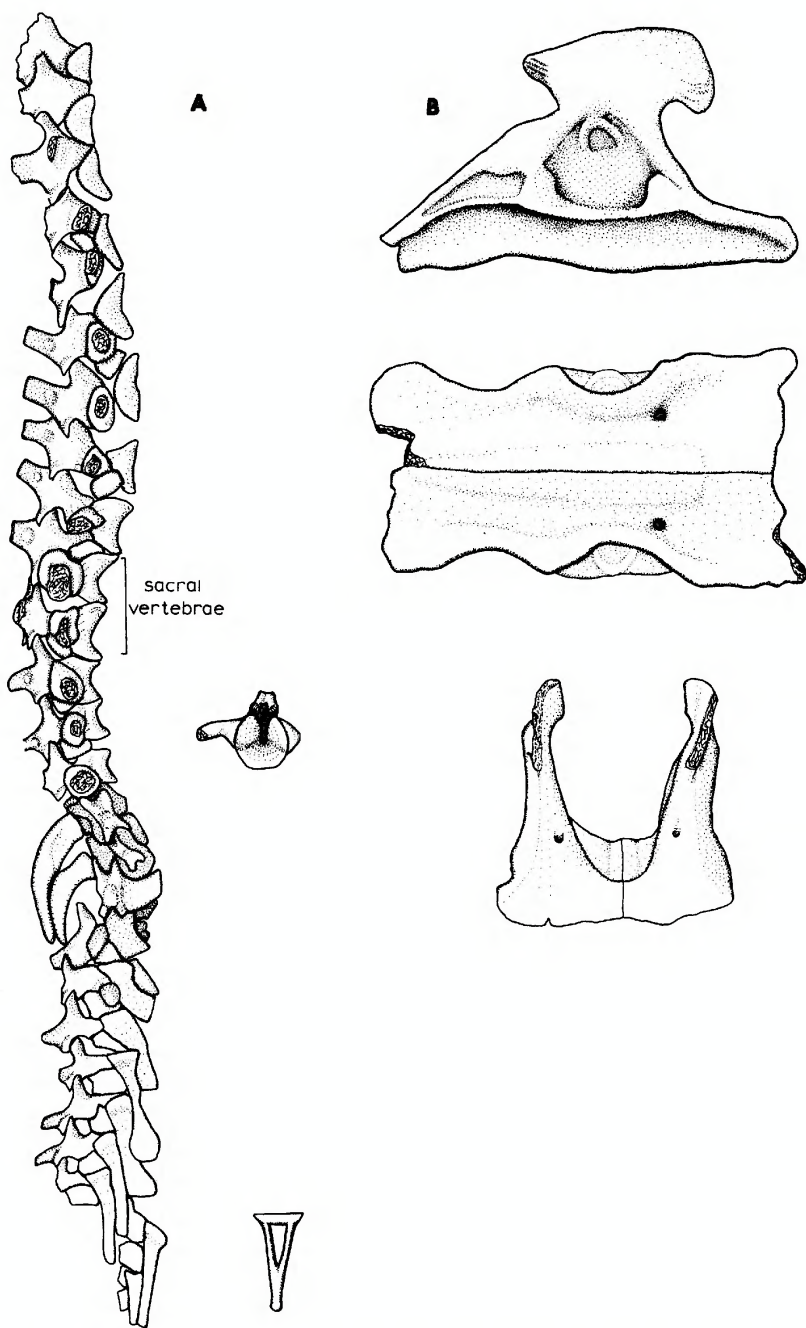


FIG. 1. *Parioxys bolli*, type, A.M.N.H. No. 7118. A. Vertebral column, anterior view of third postsacral vertebra and hemal arch. B. Pelvic girdle in lateral, ventral, and anterior views. $\times 1/2$.

FAMILY PARIOXYDAE MOUSTAFA, 1955

GENUS *PARIOXYS* COPE, 1878***Parioxys bolli***,¹ new species

TYPE: A.M.N.H. No. 7118, partial postcranial skeleton, including vertebral column and ribs, pelvic girdle and both rear limbs, ulna and radius; the only specimen known. Archer City bone bed, 1 mile southwest of Archer City, Archer County, Texas. Putnam formation, Wichita group, Lower Permian. Collector, R. V. Witter, 1945.

DIAGNOSIS: Rhachitomous amphibian similar to *Parioxys ferricolus* except for presence of posterior bifurcation of proximal end of adductor ridge of femur, greater length of tibia and fibula relative to that of femur, and lesser ossification of intercentral elements in vertebrae.

DISCUSSION: The material described by Moustafa included the remains of several individuals, all from one locality in the Belle Plains formation. Most of the skeleton is represented, but the specimens were encased in an exceedingly hard matrix which had to be ground from the surface of the bones. In many of the specimens, the surface of the bone was removed with the matrix, thus muting surface details. For this reason, the description of *P. bolli* includes many features shared by the two species, but not readily discernible in *P. ferricolus*. The only bone in which significant differences in the two species can be noted is the femur.

DESCRIPTION

AXIAL SKELETON: Twenty-four articulated vertebrae were found, with the sacral vertebrae resting within the pelvis. There are nine presacrals, two sacrals, and 13 intact postsacrals and fragments of two others. The anterior vertebrae are similar to those of *Eryops* except for having relatively shorter neural spines. More posteriorly, the intercentra are greatly enlarged, almost completely surrounding the notochord. At no point is there complete dorsal closure, as there is in the Belle Plains species. Since the Putnam specimen is larger than any of those described by Moustafa, the difference in degree of ossification cannot be attributed to the youth of this specimen. The pleurocentra remain well developed throughout the column and are not fused to the intercentra. In the region of the sacrum, the neural spines bear small lateral processes, just above the neural arch. These are present in *P. ferricolus*, but were not mentioned in Moustafa's

¹ Named for Jacob Boll, an early collector in the Texas red beds.

description. Presumably they served for areas of ligamentous attachment to strengthen the vertebral column, as do the lengthened neural spines in *Eryops*. Such processes have not been described in any other rhachitinous amphibian.

As in *P. ferricolus*, there are two sacral vertebrae, but, unlike the condition in that species, the pleurocentra do not fuse with the intercentra, and the intercentra are not complete dorsally. The first five postsacral vertebrae are like those of the trunk; behind this point, the intercentra form hemal arches. There were probably half a dozen additional tail segments which were lost in preservation.

Scattered ribs were found with the vertebrae. Those of the posterior trunk region are only three or four times the length of individual vertebrae and definitely single-headed, articulating with the transverse process of the neural arch. Posteriorly, the area of attachment extends to include the pleurocentra and, in the region of the sacrum, the intercentra. The sacral ribs are similar to those in *P. ferricolus*, with the more anterior pair the larger. The first pair of postsacral ribs extends posteriorly and, although not expanded distally, is in contact with the ilia and the posterior sacral ribs. From what is preserved of the second and third pairs of postsacral ribs, they appear to resemble those just anterior to the sacrum. The fourth, fifth, and sixth pairs are wide anteroposteriorly and extend posteriorly, rather than ventrally. They apparently served as areas for the attachment of powerful muscles for the movement of the tail. Small ribs are present on the seventh and eighth postsacral vertebrae, but none are present more posteriorly.

PELVIS: The three pelvic elements are each well ossified, and the sutures separating them are difficult to determine. The two halves are joined in a strong symphysis. The ilium forms an extensive blade, separated from the acetabulum by a constricted neck. The anterior portion of the blade extends ventrally, approaching the pubis. This ventral area was apparently missing in Moustafa's specimens. The blade is considerably thinner than the neck and bears rugose areas on the lateral surface both anteriorly and posteriorly. Its internal surface is concave anteroposteriorly and dorsoventrally in the area where the sacral ribs were attached. A low ridge extends from the middle of the lateral surface onto the supra-acetabular buttress. The latter structure extends into the acetabular area and is recessed ventrally. Anterior and posterior to the acetabulum, the ilium extends stout ridges to the pubis and ischium. The anterior ridge is considerably thickened medially. The inner surface of the acetabular area of the ilium is gently convex. The anterior and posteroventral margins of the acetabulum are formed by processes on the pubis and ischium; these

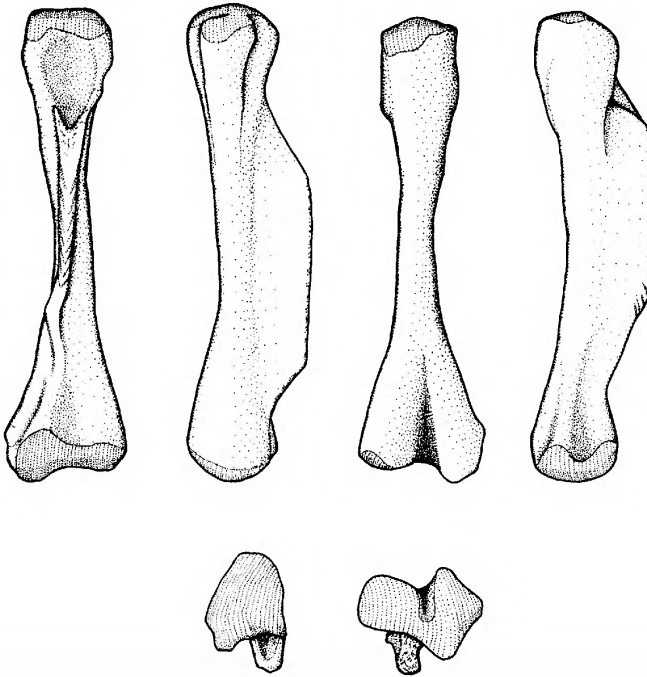


FIG. 2. *Parioxys bolli*, type, A.M.N.H. No. 7118, left femur in ventral, medial, dorsal, lateral, proximal, and distal views. $\times 1/2$.

are joined by a ridge limiting the acetabulum ventrally. Posterior to the acetabulum, the dorsal portion of the ischium tapers to the rear. The lateral surface of this triangular area is distinctly recessed between ridges along the dorsal margin of the bone and along the margin of the puboischadic plate.

The puboischadic plate is very extensive, appearing in the intact girdle as a trough with a longitudinal ridge at the base, reënforcing the symphysis. Anteriorly and posteriorly the plate thins considerably, and the reënforcement of the symphysis is reduced. The anterior and posterior margins are at approximately right angles to the line of symphysis. The anterior end of the internal surfaces of the pubes faces upward and diagonally inward, separated from the remainder of the puboischadic plate by heavy vertical ridges connecting with the ilia and bearing the small obturator foramina. Ventrolaterally, the surface of the plate is concave mediolaterally and anteroposteriorly.

FEMUR: The femur is of considerable length compared with its girth. The articular surfaces are well ossified and differ little from those of other

eryopoid amphibians. The structure of the ventral surface allows differentiation from other genera within the superfamily. A large adductor ridge stretches almost the entire distance between the proximal and distal articulating surfaces. The configuration of this ridge differs considerably in the two species. In *P. ferricolus*, the ridge is very long. Beginning just proximal to the distal articulating surface, it crosses the bone diagonally from the area of articulation with the fibula on the posterior margin and extends proximally to form the anterior boundary of the intertrochanteric

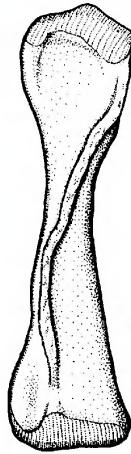


FIG. 3. *Parioxys ferricolus*, M.C.Z. No. 1545, ventral view of left femur. $\times 1/2$.

fossa. It reaches its greatest height proximal to the middle of the shaft. The ridge is slightly curved, with the anterior surface concave.

In *P. bolli*, the ridge is shorter, both proximally and distally. It is essentially straight, extending from just anterior and proximal to the area of articulation with the fibula and continuing proximally and anteriorly to the middle of the shaft—distal to the intertrochanteric fossa. Here it bifurcates. One ramus continues anteriorly, almost to the proximal articulating surface, and a second ramus extends posterior to the fossa. Between the rami is a roughened area, the fourth trochanter. The adductor ridge reaches its greatest height posterior to the middle of the shaft.

The articulating surfaces, particularly the proximal, are narrower, relative to the length of the shaft, than are those in *P. ferricolus*.

TIBIA: The length of the tibia is about 85 per cent of that of the femur, compared with 60 per cent in *P. ferricolus*, and it is much better preserved than in any of the specimens examined by Moustafa. Comparison with

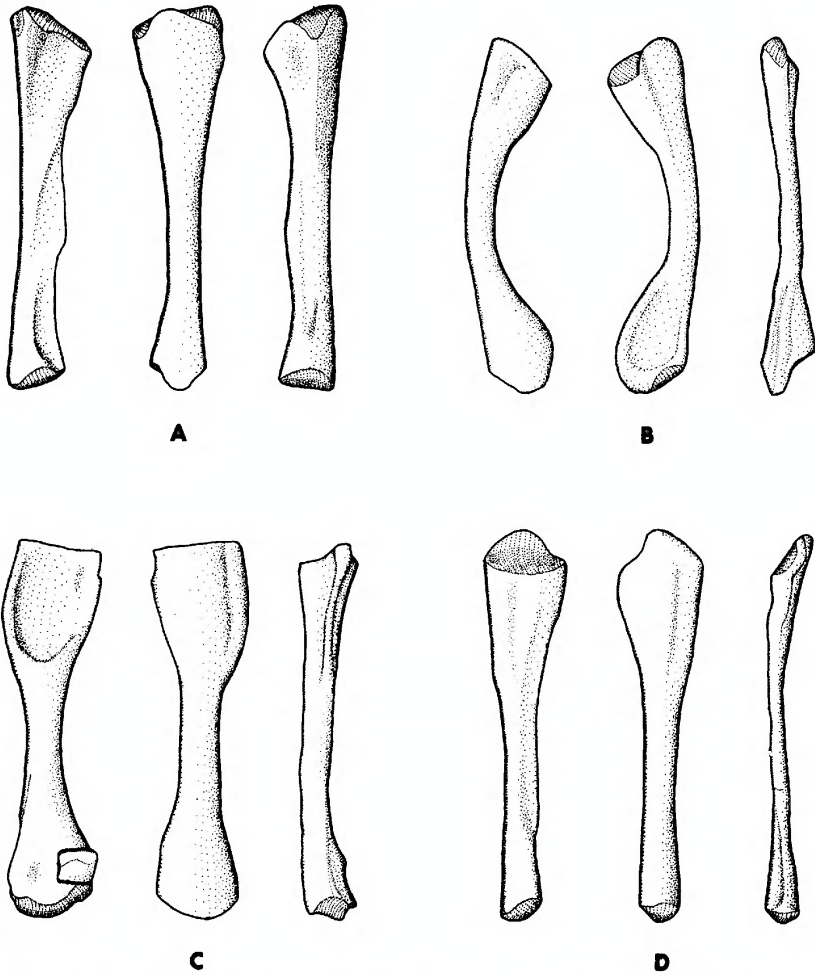


FIG. 4. *Parioxys bolli*, type, A.M.N.H. No. 7118. A. Left tibia in medial, dorsal, and lateral views. B. Right fibula in dorsal, ventral, and lateral views. C. Right radius in ventral, dorsal, and lateral views. D. Right ulna in medial, lateral, and ventral views. $\times 1/2$.

M.C.Z. No. 1545, another specimen of *P. ferricolus* from the Belle Plains formation, indicates that the tibia is essentially similar in the two species. The bone is very long compared with its width, in marked contrast to the tibia of *Eryops*. The proximal surface is expanded approximately twice as much as is the distal and has only a single articulating surface. The dorsal surface is straight and essentially flat, with no cnemial crest. There is a

thin crest on the ventral surface, running from the distal articulating surface to a point slightly proximal to the middle of the bone.

FIBULA: The fibula is very thin and strongly curved. The medial surface is strongly concave, while the lateral is moderately convex. As preserved, the bone is slightly shorter than the tibia, which probably indicates that the bone was not actually so strongly curved in life. Both proximal and distal ends are expanded mediolaterally but are little if any thicker than the shaft of the bone in a dorsoventral direction. Both proximal and distal expanded areas are convex dorsally and concave ventrally.

RADIUS: Unfortunately no humerus has been preserved, but the right ulna and radius are present. Both bones are about the same length as are the tibia and fibula. The radius, like the other limb bones, is slim, with the ends moderately expanded mediolaterally. It was adequately described by Moustafa, who also (1955a, pl. 5, fig. 2) illustrated the proximal portion of the bone.

ULNA: A bone that is apparently the ulna is present in *P. bolli*; this bone is not present in any of Moustafa's specimens, so comparison is not possible. It is very different in shape from the ulna in any other eryopsoid amphibian, but it does compare in size and general configuration with the rest of the distal limb elements in *P. bolli*. The bone is extremely thin and narrow, with very little distal expansion. The proximal area is expanded dorsoventrally, rather than mediolaterally as in other rhachitomes.¹ The olecranon is little extended beyond the end of the shaft and almost certainly finished in cartilage. The semilunar notch is ill defined. The bone is only slightly longer than the tibia. There is a very gentle ridge on the medial surface, running from the semilunar notch to the middle of the shaft. The ventral margin of the bone extends from the medial surface as a narrow ridge.

RELATIONSHIP OF *PARIOXYS FERRICOLUS* AND *PARIOXYS BOLLI*

There can be no question that the two species of *Parioxys* are closely related. Except for the configuration of the femur, the bones that are known from both species show few if any differences. Although only the two femora are present in *P. bolli*, five are known in *P. ferricolus*, all of

¹ Mediolateral flattening of the proximal end of the ulna is also found in *Araeoscelis* (Vaughn, 1955), a reptile that, like the amphibian *Parioxys*, has long epipodials relative to the length of the proximal limb bones.

which have only the anterior proximal ramus of the adductor ridge, and no fourth trochanter. The differences in the configuration of this bone, together with the lesser degree of ossification of the intercentra, appear sufficient to distinguish the two species. The Archer City bone bed is high in the Putnam formation, but is still substantially earlier than all the specimens of *P. ferricolus* from the Belle Plains. It is probable that *P. bolli* gave rise to *P. ferricolus*.

A further species, *P. romeri*, was named by Moustafa on the basis of the posterior extremity of a single humerus (M.C.Z. No. 1965) from the

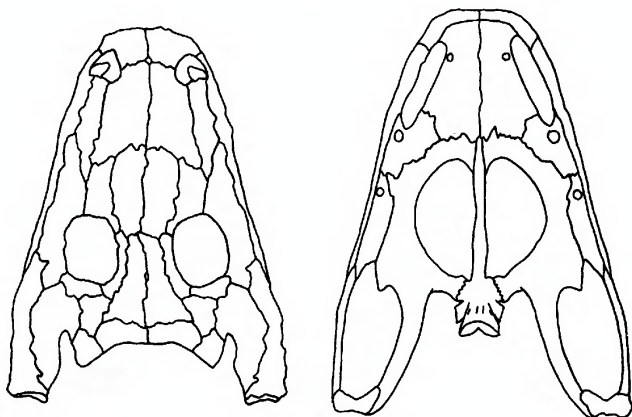


FIG. 5. *Parioxys ferricolus*, M.C.Z. No. 1162, skull in dorsal and ventral views. $\times 1/4$. From Moustafa (1955a).

Belle Plains formation. It differs from the humerus of *P. ferricolus* only in being much better preserved than any of the specimens examined by Moustafa. Until a well-preserved humerus is found with an indisputable specimen of *P. ferricolus*, it is not possible to determine whether this humerus belongs to a separate species.

AFFINITIES OF *PARIOXYS*

It is primarily on the basis of the configuration of the pelvis and the possession of two pairs of sacral ribs, as well as the lack of a fourth trochanter on the femur, that Moustafa allied *Parioxys* with the dissorophids. It is primarily on the basis of the possession of complete ring intercentra that Romer placed the genus within the Trematopsidae.

The earliest known dissorophid, *Amphibamus*, from the Pennsylvanian, has a pelvis of essentially the same configuration as that of *Eryops*. The

genus *Dissorophus*, from both the Wichita and Clear Fork beds, retains this primitive type of pelvis. Only the genera *Broiliellus* and *Cacops* are known to have attained a pelvis similar in configuration to that of *Parioxys*, and only the genus *Cacops* from the Clear Fork has two pairs of sacral ribs. Hence neither an enlarged iliac blade, with an essentially horizontal puboischiadic plate, nor the possession of two pairs of sacral ribs is typical of the family Dissorophidae. The possession of a posterior proximal ramus of the adductor ridge in *P. bolli*, and the presence of a fourth trochanter, further separate the genus from dissorophids, which do not show these features even in the later Middle Pennsylvanian genera. It seems much more likely that these were primitive features in *Parioxys* and later lost, rather than being developed during the course of evolution of the genus, and secondarily lost. Since the features that Moustafa used to ally the dissorophids with *Parioxys* have developed separately within the two groups, these characters cannot be cited to indicate close relationship.

The same is true for the character cited by Romer in classifying the genus in the Trematopsidae. The genus *Acheloma* from the Wichita has crescent-shaped intercentra which become complete only in the Clear Fork genus *Trematops*. As we have seen from the description of *P. bolli*, the encirclement of the notochord by the intercentra in *Parioxys* is not achieved until the Belle Plains, while the Putnam species has not yet reached this stage in development.

It appears unlikely that *Parioxys* can be allied with either of these families on the basis of the characters mentioned. Nor are there any other features that relate the genus to any particular eryopoid family. The wisest course at present seems to be to place *Parioxys* in a family of its own, as suggested by Moustafa, but within the superfamily Eryopsoidea, since the features by which the superfamily has been defined by Romer (1947, p. 313) apply equally well for the Parioxydae and for the remaining four families.

ACKNOWLEDGMENTS

I wish to thank Prof. Alfred Sherwood Romer, of the Museum of Comparative Zoölogy of Harvard College, for drawing my attention to the specimen of *Parioxys bolli*, which is currently at Harvard, and for discussions with him concerning its affinities. I also wish to thank Dr. Edwin H. Colbert, Chairman of the Department of Vertebrate Paleontology of the American Museum of Natural History, for permission to describe the specimen.

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